Strength Determines Coalitional Strategies in Humans

Strength Determines Coalitional Strategies in Humans

Joyce F. Benenson[1,2], Henry Markovits[3], Melissa Emery Thompson[4], Richard W. Wrangham[2]

1. Department of Psychology, Emmanuel College, 400 The Fenway, Boston, MA 02115, USA
2. Department of Biological Anthropology, Harvard University, 15 Divinity Avenue, Cambridge, MA 02138, USA
3. Département de Psychologie, Université du Québec à Montréal, C.P. 8888, Succ Centre-Ville, Montréal, QC H3C 3P8, Canada.
4. Department of Anthropology, MSC01-1040, University of New Mexico, Albuquerque, New Mexico 87131

Correspondence to: Joyce Benenson[1,2] (e-mail: Joyce.Benenson@gmail.com)

Running Head: Coalitional strategies

Abstract

Coalitions enhance survival and reproductive success in many social species, yet they generate contradictory impulses. Whereas a coalition increases the probability of successfully obtaining rewards for its members, it typically requires a division of rewards between members, thereby diminishing individual benefits. Non-human primate data indicate that coalition formation is more likely when an individual's probability of success is low when competing alone. No comparable studies exist for humans. Here we show using a computerized competitive game that humans exhibit a systematic, intuitive strategy for coalition formation based on their own and others' levels of strength, a pattern that resembles coalition formation in chimpanzees, *Pan troglodytes*. Despite equal expected pay-offs for all strategies, subjects were more likely to form coalitions as their own level of strength waned. Those chosen as coalition partners tended to be stronger individuals or arbitrarily-designated "friends." Results suggest a heuristic for human coalitionary decisions that does not rest on calculations of payoffs in the immediate context.

Key Index Words: Coalitional Strategies, Strength, Friendship, Cooperation

Much research in behavioral economics focuses on games in which humans tend not to maximize personal payoffs, thereby defying rational expectations (Kahneman & Tversky, 1979; Camerer & Fehr, 2006). Studies of this phenomenon in cooperative games have focused on explaining the occurrence of altruism, because individuals often pay a cost to reward cooperative behavior or impose sanctions on selfish behavior (Fehr & Fischbacher, 2003). Explanations for such bounded rationality range from cultural group selection, where the strategies of a few influence those of a majority (Fehr & Fischbacher, 2003), to natural selection for "fast and frugal" heuristics that outperform other strategies in the long-term (Trivers, 2006; Gigerenzer, 2008). Here we extend the study of cooperative behavior to coalition formation among non-kin. We test the hypothesis that humans exhibit heuristic strategies for deciding when to form coalitions, and for choosing coalition partners.

Coalitions previously have been studied with respect to the bargaining strategies between assigned coalition partners (Kalisch, Milnor, Nash, & Nering, 1954; Rapoport & Kahan, 1976; Zwick & Rapoport, 1985). Our study uses a simple economic game, in which all strategies produce equal payoffs, to ask under what conditions humans tend to form coalitions, and whether they show preferences for particular types of partners. Our main hypothesis, based on studies of chimpanzee coalitions by Watts (1998), is that the probability of forming a coalition is inversely related to level of personal strength, defined as the probability of success when competing alone.

We define a coalition as two or more individuals acting cooperatively to compete against a third party (Harcourt & de Waal, 1992). Whereas in many species a shared genetic interest promotes cooperation due to kin selection (Hamilton, 1964), cooperation with non-kin is less common and subject to numerous potential influences. Mathematical models indicate that whether an individual joins a non-kin coalition depends on level of personal strength, affinity between partners, awareness of conflicts, winner and loser effects, fighting costs, and the synergy versus antergy of the coalition (Dugatkin, 1998; Johnstone & Dugatkin, 2000; Mesterton-Gibbons & Sherratt, 2006; Gavrilets, Duenez-Guzman, & Vose, 2008). These models further predict thresholds at which individuals facultatively switch from an individual to a coalitional strategy (Mesterton-Gibbons & Sherratt, 2006; Gavrilets et al., 2008).

Empirical tests of these variables with primates are rare, but in a study of coalitionary mate guarding by wild chimpanzees *Pan troglodytes* Watts (1998) showed a link between level of personal strength and coalition formation. The number of adult males in a group varied from 1 to more than 20. The highest-ranking male present was often successful in monopolizing matings with estrus females, but his probability of success fell as the number of competing males increased. Consistent with models predicting a threshold effect for coalition formation (Mesterton-Gibbons & Sherratt, 2007; Gavrilets et al., 2008), Watts (1998) showed that the highest-ranking chimpanzees appeared to follow a decision rule for coalition formation: When their individual mating success declined below 50%, they formed dyads (coalitions with one high-ranking partner) that successfully excluded all other males from mating; when it fell below 33%, they formed triads (coalitions with two partners) that were again successful in excluding other males. Although the division of matings ("rewards") within a coalition was often unequal, males were relatively tolerant of mating efforts by their coalition partners. These strategies enabled members of coalitions to increase their mating access relative to competitors (Watts, 1998).

Other research with primates demonstrates that high-ranked individuals tend to be the most attractive coalition partners, presumably because they maximize the combined strength of a coalition (Duffy, Wrangham, & Silk, 2007). For example when low-ranking animals intervene in conflicts they tend to support the higher-ranking of two contestants (Perry, 1996; Chapais & St-Pierre, 1997; Silk, Alberts, & Altmann, 2004). A partner's level of strength therefore also influences coalition formation.

Further, while coalitions with non-kin occur both opportunistically and with long-standing social partners, preferential coalitions with "friends" occur in both male and female chimpanzees as well as other primates (de Waal, 1982; Boesch & Boesch-Achermann, 2000; Mitani, 2006), such as vervets (*Cercopithecus aethiops sabaeus*) (Hunte & Horrocks, 1987) and Japanese macaques (*Macaca fuscata*) (Chapais & St.-Pierre, 1997). This influence of relationship quality can be due to close associates having high mutual tolerance. In laboratory studies, chimpanzees chose to cooperate more often with social partners who were more likely to share their rewards from collaborating (Melis, Hare, & Tomasello, 2006). Male chimpanzees also engage in inter-group boundary patrols and form intra-group coalitions more frequently with those with whom they groom and maintain close proximity (Watts & Mitani, 2001). Thus preference for high rank and for friends occurs in both sexes and across a variety of species.

Given the importance of level of personal strength, partner's level of strength, and relationship quality to coalitions of monkeys and apes, we tested the hypothesis that these factors would affect coalition formation in humans. We also examined explicitly whether a threshold effect emerges for coalition formation following a rule similar to the one proposed by Watts (1998) for chimpanzees: After probabilities of individual gain dip below 50%, switch to a coalitional strategy and divide rewards with one partner. To this end, we designed a computerized game to examine under what conditions a subject chooses to form a coalition.

Experiment 1

Method

61 male and 63 female subjects individually competed for money (maximum $5) against two fictional same-sex opponents (labeled “friend” or “non-friend”) in 28 rounds of a computerized game. On each round, the player competed against the two opponents for 100 points (for a total of 2800 points distributed amongst the player and two opponents over the entire game). Each round, the player’s level of Personal Strength (probability of winning all 100 points in a round when competing alone) varied randomly from 20-80% (in 10% increments) with 4 instances of each level of Personal Strength. On every round, the sum of the player’s level of Personal Strength plus the levels of strength of the two opponents (each opponent’s probability of winning all 100 points in the round) equaled 100%, with the levels of the two Opponents’ Strengths unequally apportioned. On half of the rounds, the stronger opponent was the friend, whereas on the other half the stronger opponent was the non-friend. Half of the subjects played under competitive instructions, with only the player earning the highest number of points winning money. The other half played under non-competitive instructions in which all earned points were converted to money. The players were told how much they had won only after the game had ended.

On each round the player was informed of his/her own level of Personal Strength (probability of winning the 100 points on that round by competing alone) and the levels of each of the two Opponent's Strengths, and was given three choices: (1) Compete alone, with level of Personal Strength indicating probability of winning the 100 points; (2) Form a coalition with either one of the two opponents, with levels of Personal Strength and Opponent's Strength summed to generate their Coalitional Strength (combined probability of winning the 100 points on that round by competing together), and if the coalition won, divide the points proportionally according to Personal Strength versus Opponent's Strength; or (3) Avoid competing by dividing the 100 points on that round amongst the player and the two opponents according to the levels of strengths of each, thereby guaranteeing a payoff for everyone. While summing the levels of strength of the players may not provide a perfectly accurate simulation of Coalitional Strength, little empirical data exist regarding the precise advantage that accrues to a coalition relative to that of individuals, and theoretical models reach differing conclusions (Adams & Mesterton-Gibbons, 2003; Mesterton-Gibbons & Sherratt, 2007). Consequently, we chose a simple additive model.

Levels of Personal Strength (probabilities of winning by competing alone) were clearly demonstrated before the game. Although each choice in a given round produced identical expected payoffs, players were not told this explicitly. Instead, after describing the three choices a player confronted, we illustrated the expected payoffs for each choice using a concrete example in which the player had a Personal Strength of 60 and one Opponent's Strength was 30 and the other Opponent's Strength equaled 10. In the illustration, the player therefore had a 60% probability of winning the 100 points alone, and the two opponents had 30% and 10% probabilities of winning the 100 points alone, respectively. Thus, if the player chose to play alone, the player would have a 60% chance of winning 100 points (producing an expected payoff of 60). If the player formed a coalition with the opponent with the 30% probability of winning, their Coalitional Strength or combined probability of winning the 100 points increased to 90%. Should they win the 100 points, the points would be divided proportionally according to their individual strengths or probabilities of winning (60:30), thereby yielding twice as many points for the player as for the coalition partner, in this case 67:33. (Thus, the player's expected payoff again equaled 60 (90% of 67 points).) Finally, if the player chose a guaranteed payoff of points by allying with both opponents, then the player and the two opponents received the number of points that corresponded to their individual levels of strength or probabilities of winning alone, in this instance 60 points for the player with the two opponents receiving 30 and 10 points, respectively. (Therefore, the player's expected payoff once again equaled 60.) To facilitate understanding and increase the ecological validity of the game, on each round the player and two opponents were depicted by three identical same-sex cartoon faces with the words "Me," "Friend," and "Non-Friend" displayed beneath one of each of the faces (with the friend and non-friend alternating directional positions on each round and the player's face always centered), and the strengths or probabilities of winning indicated above the faces.

Results

The Influence of Level of Personal Strength (Probability of Winning Alone)

We conducted an initial repeated measures analysis of variance (ANOVA) on the percent of choices competing alone at each level of Personal Strength, with Sex and Instruction (competitive or non-competitive) as independent variables. An individual could choose to compete alone from 0 to 4 times per level of Personal Strength, so a percentage of competing alone was computed for each individual at every level of Personal Strength. A linear contrast analysis demonstrated that Personal Strength influenced choice of competing alone with stronger players competing alone more frequently, $F_{1,120}$=202.77, P<.0001 (see Figure 1).

Players who chose not to compete alone could either form a coalition and increase their probability of winning something, or accept a guaranteed payoff of points that corresponded to their level of Personal Strength on that round. Again, an individual could choose to form a coalition or select a guaranteed payoff from 0 to 4 times per level of Personal Strength, so the percentage of coalition formation decisions and guaranteed payoffs was computed for each individual at every level of Personal Strength. To examine the percentages of coalitional choices and guaranteed payoffs, we conducted a repeated measures ANOVA with two repeated factors, Type of choice (percent coalitions versus percent guaranteed payoffs) and level of Personal Strength with Sex and Instruction as independent variables. A linear contrast best explained the effect of Personal Strength: Weaker players both formed more coalitions and chose more guaranteed payoffs, $F_{1,120}$=228.32, P<.0001 (see Figure 1). At all levels of Personal Strength however, players preferred to form a coalition with one opponent (X=54.55, SD$\pm$24.22, N=124) over guaranteed payoffs of points for everyone (X=10.48, SD$\pm$18.36, N=124, $F_{1,720}$=198.30, P<.0001).

Additionally, three interactions, Level of Personal Strength X Type of choice $F_{6,720}$=22.33, P<.0001, Level of Personal Strength X Instructions, $F_{6,720}$=3.60, P=.002, and Type of choice X Instructions, $F_{1,120}$=5.44, P=.02, were significant, but were qualified by a 3-way interaction between Type of choice X Level of Personal Strength X Instructions interaction, $F_{6,720}$=4.01, P=.001. Follow-up Tukey's tests (P<.05) showed players accepted guaranteed payoffs more often under non-competitive than competitive instructions at their three lowest levels of Personal Strength: 40, 30, and 20.

Threshold of Level of Personal Strength for Ceasing to Compete Alone

We next examined whether players exhibited thresholds of Personal Strength at which they ceased to compete alone. Of 124 subjects, 106 (85.5%) ceased competing alone at a specific level of Personal Strength (probability of winning alone) and never competed alone beneath that level of Personal Strength. By contrast, 5 (4.0%) competed alone on every round and 13 (10.5%) displayed no clear strategy. Figure 2 displays the percentage of individuals of the total (124) who ceased competing alone at each level of Personal Strength (probability of winning). As shown in the figure, the majority of individuals ceased competing alone when their probability of winning alone declined to 50% or below. In other words, 85% of individuals intuitively decided that risking competing alone to win all the points was worthwhile only above a specific probability of winning and never below that level. These thresholds of Personal Strength for competing alone emerged despite the random distribution of levels of Personal Strength that the players confronted across rounds.

Further, the distribution of the number of individuals who ceased competing alone at each level of Personal Strength differed from randomness ($X^2(6)$=24.49, P=.0004, two-tailed). The levels of Personal Strength at which players switched from an individualistic to a coalitional strategy, or to guaranteed payoffs, tended to be intermediate. This indicates that a large proportion of individuals found it aversive to compete alone when their own Personal Strength or probability of winning alone diminished below a set point. They therefore switched either to forming a coalition or accepting guaranteed payoffs for themselves and their opponents.

The Effect of Level of Opponent's Strength and Friendship on Coalition Formation

We then examined coalitional choices to determine the effects of the level of Opponent's Strength (opponent's probability of winning alone) and Friendship with the player. Omitting those who competed alone on a round or chose guaranteed payoffs, the percent of individuals who made coalitional choices for the stronger versus weaker opponent, and friend versus non-friend, were compared in an ANOVA with Sex and Instructions as independent variables and level of Opponent's Strength (strong versus weak) and Friendship (friend versus non-friend) as repeated factors. Players formed coalitions more often with strong opponents ($X=33.20$, $SD \pm 12.41$, $N=117$) than weak ones ($X=16.80$, $SD \pm 12.41$, $N=117$, $F_{1,113}=51.30$, $P<.0001$), and despite the fact that the designation of "friend" was completely arbitrary, players were more likely to form coalitions with a player labeled friend ($X=33.55$, $SD \pm 11.44$, $N=117$) than non-friend ($X=16.45$, $SD \pm 11.44$, $N=117$, $F_{1,113}=64.80$, $P<.0001$). Level of Opponent's Strength (opponent's probability of winning alone) and Friendship formed an additive model: strong friend ($X=42.52$, $SD \pm 17.22$, $N=117$), weak friend ($X=24.58$, $SD \pm 18.67$, $N=117$), strong non-friend ($X=23.87$, $SD \pm 20.48$, $N=117$), and weak non-friend ($X=9.03$, $SD \pm 13.11$, $N=117$). Tukey's tests on a significant interaction between levels of Opponent's Strength X Friendship X Sex, $F_{1,113}=4.89$, $P=.029$, did not yield significant differences.

To determine whether the decision rules used were consciously available, we conducted a second study.

Experiment 2

Method

26 new subjects were presented with the same task as in Experiment 1, without actually being asked to play and with no offer of monetary rewards. Using a powerpoint presentation, all subjects were shown the same computer screens as in the actual study and provided with the competitive set of instructions. The same illustration of the probabilities and payoffs was provided, and subjects were queried verbally regarding their understanding of the payoffs. All indicated that they understood the probability structure and the principle of unequal splits. Then, the computer screen displayed the 28 rounds in descending order of the player's level of Personal Strength and asked each individual to record on paper the best strategy for a player to earn the most points on each round.

Results

Not a single subject chose the strategy used by the subjects who actually played the game, with the exception that Friendship was predicted by all subjects to positively influence coalition formation. Rather, 12/26 (46.15%) subjects suggested either coalition formation or guaranteed payoffs at all levels of Personal Strength; 11/26 (42.32%) subjects recommended forming a coalition only when level of Personal Strength was high; one subject recommended only competing alone; and two subjects did not exhibit a consistent strategy, although both occasionally suggested forming a coalition with a weak opponent to offset the level of strength of the strongest opponent. This test therefore demonstrates that the conditional strategy obtained in the actual study is neither obvious nor conscious.

Discussion

Our data show that humans followed a consistent strategy whereby individuals who were strong (had a high probability of winning all the points alone) competed alone until their level of strength waned, then formed a coalition with a stronger and/or friendlier opponent. When the individual's level of strength declined too far, the individual was more likely to accept fate with a minimal, but guaranteed reward. The same strategy was followed under both the competitive and non-competitive conditions, although individuals playing under the competitive condition switched to guaranteed payoffs at lower probabilities of winning than individuals playing under non-competitive conditions. This indicates that the strategy for forming coalitions applied across conditions, despite small compensations for changes in the ecology.

Further, 85% of individuals exhibited a threshold for ceasing to compete alone and permanently switching to a coalitional strategy or guaranteed payoffs. The majority of individuals ceased competing alone and switched to a coalitional strategy or guaranteed payoffs after their probability of winning alone decreased to 50% or below. In other words, individuals competed alone only above an intermediate probability of winning, centered around 40-50%. At lower probabilities of winning alone, they always formed coalitions or chose guaranteed payoffs with the other two players. The threshold effect occurred despite random fluctuations in the probabilities of winning alone. Thus, individuals followed a powerful rule predicated on personal strength or probability of winning alone that guided their decision-making process.

Finally, when individuals did form coalitions, they preferentially selected stronger and friendlier opponents. This occurred even though coalition formation aided their opponents' probabilities of obtaining payoffs and despite explicit competitive instructions that only the player with the highest number of points would win.

These findings with human subjects strongly resemble coalitionary behavior of chimpanzees. First, chimpanzees appeared to follow clear decision-making rules for coalition formation predicated on personal strength in which high-ranked individuals switched from competing alone to forming a coalition with the next strongest individual when their probability of success declined to 50% (Watts, 1998). Second, a clear threshold effect emerged, such that high-ranked chimpanzees continued to form coalition formations when their probability of success remained at or below 50% (Watts, 1998). Finally, several studies demonstrate that chimpanzees were more likely to form coalitions with opponents who were stronger and friendlier (de Waal, 1982; Boesch & Boesch-Achermann, 2000; Melis et al., 2006; Mitani, 2006; Duffy et al., 2007).

Given that in the current game expected payoffs were identical for each choice and hence no rationale existed for selecting one strategy over another on any given round, the consistency of these results strongly implies the operation of a heuristic governing such behavior, similar to other types of heuristics observed in studies of behavioral decision-making (Kahneman & Tversky, 1979; Gigerenzer, 2008). That the current results resemble so closely chimpanzees' coalitional strategies for mate guarding (Watts, 1998) suggests an evolved heuristic that conferred a selective advantage over time (Mesterton-Gibbons & Sherrat, 2007).

Individual differences in thresholds for coalition formation may result from a number of factors. Individual fighting strength likely determines when an individual perceives his level of strength to be lower than this threshold and hence decides to switch to a coalitional strategy (Mesterton-Gibbons & Sherratt, 2006; Gavrilets et al., 2008). Weak individuals may be responsive to such factors as prohibitively high expected costs of conflict, thereby inducing them to accept any reward no matter how small (Mesterton-Gibbons & Sherratt, 2007; Gavrilets et al., 2008).

Critically however, not all individuals may have the opportunity to form coalitions. For chimpanzees and humans, high-ranked individuals, who provide the greatest increase in the certainty of obtaining rewards, may make the most attractive coalition partners. Thus, high-ranked individuals likely find coalition-building easier than lower-ranked individuals, simply because they are more popular as coalition partners. Popularity of an individual then may depend both on the individual's capacity to obtain a reward within a given ecology and on the individual's willingness to share it with a coalition partner. Friends likely also make better coalition partners, possibly because of the greater mutual trust that has been established between them, thereby reducing the costs of coalition formation (Melis et al., 2006; Gavrilets et al. 2008).

Individual differences also likely influence perceptions of strength and hence coalition formation. In humans, dominance rank (Sapolsky, 2005) and inhibition (Schwartz, Wright, Shin, Kagan, & Rauch, 2003) likely influence perceptions of personal strength and subsequent decisions about coalition formation and potential partners. Interestingly, we found no sex differences in our analyses. This suggests that human males and females use similar decision rules for forming coalitions, though differences in male and female status structures could affect the use of coalitions in practice.

Differing ecologies also likely influence perceptions of level of strength. In conditions of scarcity, including food shortages or population increases, individuals of all ranks may be more prone to attempt to form coalitions or to accept small rewards through guaranteed payoffs. Support for the importance of the ecology stems from the finding in the current game that individuals in the competitive condition chose guaranteed payoffs at lower probabilities of winning compared to individuals in the non-competitive condition. Intuitively, individuals in the explicitly competitive condition likely believed that not providing rewards to the second opponent increased their own advantage.

The observed heuristic can also be viewed partially within the general framework of risk aversion. The current heuristic cannot be predicated solely on avoiding risk, because otherwise individuals would always select guaranteed payoffs by sharing the points with the two opponents. Understanding the components of risk aversion and how this affects decision-making constitutes a complex problem (Davies & Satchell, 2007). An often-used index of risk is the "risk premium," the amount by which the expected value (EV) of a gamble exceeds a guaranteed payoff. In the present study, the risk premium is 0, since in all cases, the EV and the amount that can be obtained with certainty are identical. For example, when an individual's level of strength is 20, EV equals 20. By allying with the two other players, they can gain 20 with certainty. By this definition, risk aversion cannot explain the current findings.

If we simply equate risk with uncertainty however, then our results can be described as consistent with a model of risk tolerance. When individuals have a high probability of winning alone (and thus low uncertainty), they will choose to risk competing alone to gain all the rewards rather than ensuring a high certain payoff. When their probability of winning alone decreases sufficiently, they can maintain a low level of uncertainty by preferentially forming a coalition with one other, even though their rewards must now be divided with the coalitional partner. It is only when their uncertainty rises sharply, that is their probability of winning alone becomes extremely small, that they opt for a total reduction of uncertainty and accept a small, but guaranteed reward. A potential explanation of this pattern consistent with Kahneman and Tversky's (1979) prospect theory is that individuals who have a high probability of winning underestimate their subjective risk, whereas those with a lower probability of winning overestimate subjective risk. Future research is required to investigate this possibility.

In natural environments, some species of animals appear predisposed to form coalitions when an individual cannot succeed without the strength of another (Clutton-Brock, 2002; Mesterton-Gibbons & Sherratt, 2006).The heuristic identified here however does not apply across primate species. For example, in savanna baboons (*Papio cynocephalus*), low- or middle-ranked males form coalitions with others of similar rank against a high-ranking male (Bercovitch, 1988). In this study, humans bypassed a strategy whereby they could have formed a coalition with a weaker opponent that would have diminished the strongest individual's probability of winning. Individuals also did not choose to compete alone at the lowest probabilities of winning to at least attempt to beat stronger opponents, nor did they select guaranteed payoffs at the highest probabilities of winning, thereby ensuring that they would beat their opponents on those rounds. Finally, only a few individuals competed alone on all rounds, a high-risk, high-gain strategy. Understanding the reasons some species form coalitions, and the contexts in which they occur, will provide greater insight into the ways in which humans' coalition-building decisions resemble and differ from those of other species.

In summary, this study provides clear evidence using a simple economic game that perceived probability of winning determines an individual's willingness to form coalitions. Similarities in decisions about coalition formation between humans and our closest genetic relatives support the hypothesis that the principles of human cooperation are rooted in our evolutionary past. Our results indicate the presence of a simple heuristic rule guiding coalition formation that provided no rationale for forming coalitions or choosing particular partners. Our paradigm therefore offers opportunities to examine heuristics for coalition formation in humans under varying physical and social conditions with individuals who vary in personal characteristics.

References

Adams, E. S. & Mesterton-Gibbons, M. (2003). Lanchester's attrition models and fights among social animals. *Behav. Ecol*. **14**, 719-723.

Bercovitch, F. E. 1988. Coalitions, cooperation, and reproductive tactics among male baboons. *Anim. Behav*. **36**, 1196-1209.

Boesch, C. & Boesch-Achermann, H. 2000. *The chimpanzees of the Tai forest*. Oxford University. Press.

Camerer, C. F., & Fehr, E. 2006. When does "economic man" dominate social behavior? *Science* **311**, 47-52.

Chapais, B. & St.-Pierre, C. G. 1997. Kinship bonds are not necessary for maintaining matrilineal rank in captive Japanese macaques. *Int. J. Primatol*. **18,** 375-385.

Clutton-Brock, T. 2002. Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* **269**, 69-72.

Davies, G. B. & Satchell, S. E. 2007. The behavioural components of risk aversion. *J. Math. Psychol*. **51**, 1-13.

Duffy, K. G., Wrangham, R. W., & Silk, J. B. 2007. Male chimpanzees exchange political support for mating opportunities. *Curr. Biol*. **17**, 586-587.

Dugatkin, L. A. 1998. A model of coalition formation in animals. *Proc. R. Soc. Lond. B* **265**, 2121-2125.

Fehr, E. & Fischbacher, U. 2003. The nature of human altruism. *Nature* **425**, 785-791.

Gavrilets, S., Duenez-Guzman, E. Z., & Vose, M. D. 2008. Dynamics of alliance formation and the egalitarian revolution. *PLOS ONE* **3**, e3293, 1-9.

Gigerenzer, G. 2008. Why heuristics work. *Perspect. Psychol. Sci*. **3**, 20-29.

Gilby, I. C. 2006. Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Anim. Behav*. **71**, 953-963.

Harcourt, A. H. & de Waal, F. B. M. 1992. *Coalitions and alliances in humans and other animals.* Oxford Univ. Press, Oxford.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1-16.

Hunte, W. &. Horrocks, J.A. 1987. Kin and non-kin interventions in aggressive disputes of vervet monkeys. *Behav. Ecol. and Sociobiol*. **20**, 257-263.

Johnstone, R. A. & Dugatkin, L. A. 2000. Coalition formation in animals and the nature of winner and loser effects. *Proc. R. Soc. Lond. B* **267**, 17-21.

Kahneman, D. & Tversky, A. 1979. Prospect theory: An analysis of decision under risk. *Econometrica* **47**, 263-291.

Kalisch, G. K., Milnor, J. W., Nash, J. F., & Nering, E. D. 1954. Some experimental n-person games. In *Decision processes* (ed. R. M. Thrall, C. H. Coombs & R. L.Davis, R. L.). pp. 301-327. John Wiley and Sons.

Melis, A. P., Hare, B., & Tomasello, M. 2006. Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Anim. Behav.* **72**, 275-286.

Mesterton-Gibbons, M., & Sherratt, T. N. 2006. Coalition formation: a game theoretic analysis. *Behav. Ecol*. **18**, 277-286.

Mitani, J. C. 2006. Demographic influences on the behavior of chimpanzees. *Primates* **47**, 6-13.

Perry, S. 1996. Female-female social relationships in wild white-faced capuchin monkeys. *Am. J. Primatol.* **40**, 167-182.

Rapoport, A. & Kahan, J. P. 1976. When three is not always two against one: Coalitions in experimental three-person games. *J. Exp. Soc. Psychol*. **12**, 253-273.

Sapolsky, R. M. 2005. The influence of social hierarchy on primate health. *Science* **308**, 648-652.

Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., Rauch, S. L. 2003. Inhibited and uninhibited infants 'grown-up': Adult amagladar response to novelty. *Science* **300**, 1952-1953.

Silk, J. B., Alberts, S. C., & Altmann, J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Anim. Behav*. **67**, 573-582.

Trivers, R. 2006 Reciprocal altruism: 30 years later. In *Cooperation in primates and humans* (ed. P. M. Kappeler & C. P. van Schaik). pp. 67-83. Springer.

de Waal, F. B. M. 1982. *Chimpanzee politics*. Johns Hopkins Press, Baltimore.

Watts, D. P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav. Ecol. and Sociobiol*. **44**, 43-55.

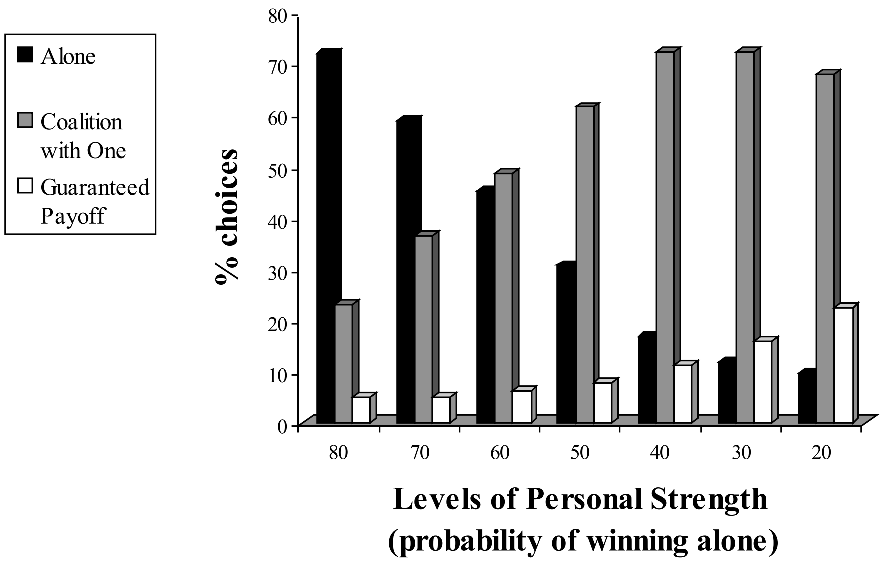
Watts, D. P. & Mitani, J. C. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* **138**, 299-327.

Zwick, R. & Rapoport, A. 1985. Relative gain maximization in sequential 3-person characteristic function games. *J. Math Psychol*. **29**, 333-359.

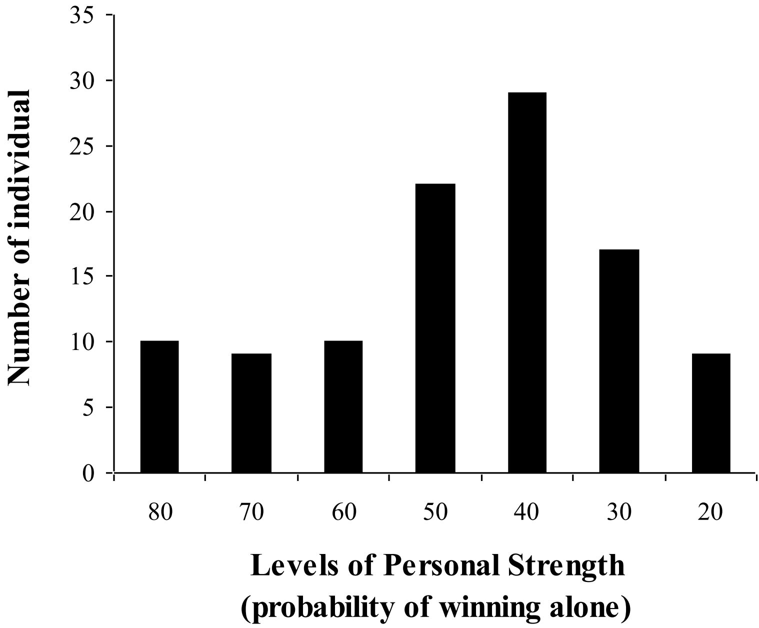
Figure Captions

Figure 1. Percentage of choices competing alone, in a coalition, or with a guaranteed payoff at each level of Personal Strength (probability of winning alone).

Figure 2. Number of individuals at each level of Personal Strength who ceased competing alone at that level of Personal Strength and at all lower levels and henceforth only chose coalitional strategies or guaranteed payoffs.



Alone
Coalition with One
Guaranteed Payoff
% choices
0
10
20
30
40
50
60
70
80
80
70
60
50
40
30
20
Levels of Personal Strength
(probability of winning alone)


35
30
25
20
15
10
5
0
Number of individual
80
70
60
50
40
30
20
Levels of Personal Strength
(probability of winning alone)